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Marine ecosystem variability and human community responses: The example of Ghana, West Africa

R. Ian Perry[a,*], U. Rashid Sumaila[b]

[a]Pacific Biological Station, Fisheries & Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC, Canada V9 T 6N7
[b]Sea Around Us Project, Fisheries Economics Research Unit, Fisheries Centre, University of British Columbia, 2259 Lower Mall Road, Vancouver, BC, Canada V6 T 1Z4

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Abstract

This study describes variability in the marine ecosystem of Ghana, West Africa, on several temporal and spatial scales and discusses how the human communities using this ecosystem respond to this variability to cope socially and economically. Ghanaian marine waters are part of an upwelling system with strong seasonal and inter-annual variability. Much of this variability is forced at large spatial scales in the tropical Atlantic and by El Niño—Southern Oscillation events in the Pacific Ocean, which influence inter-annual variability of sea surface temperature and pelagic fish landings off Ghana. At decadal scales, Ghanaian marine waters experienced cool sea temperatures and low fishery landings during the 1960s, rapid warming and increases in fishery landings during the late 1970s and 1980s, and variable temperatures and fishery landings during the 1990s. In the late 1990s, pelagic and demersal fish populations appeared to be declining, partly due to over-fishing, although the per capita supply (domestic production plus net imports) of fish was kept high by increased imports. Artisanal fishers and fishing communities in Ghana have devised strategies to deal with variability on seasonal and inter-annual scales. These livelihood strategies include: (i) exploiting marine and terrestrial natural resources more intensively, initially at local scales but expanding to regional scales; (ii) ensuring multiple and diversified income sources; (iii) investing in social relationships and communities for support; and (iv) undertaking seasonal or permanent migrations. In addition, the national government imports fish to deal with shortages. However, these strategies may be less adapted to variability at decadal scales, and may not be sustainable when viewed at the larger scales of environmental change.

Keywords: Fisheries; Guinea Current Livelihood strategies; Spatial scales; Temporal scales; Upwelling; West Africa

1. Introduction

Marine ecosystems are naturally variable from seasonal to inter-decadal scales. Over the past decades, however, it has become clear that direct human activities, such as intensive fishing, have provided an additional source of variability to these ecosystems. Indirect human actions that cause global warming are now inducing further uncertainty to marine ecosystems. Variability in marine ecosystems generates uncertainty in the human communities that interact with and depend upon marine resources. It is usually assumed that these communities have, over the long term, evolved strategies to accommodate natural marine variability, but it is an open question as to whether these "traditional" coping strategies will be sufficient to preserve the historical interaction between human communities and the sea when faced with conditions of both intensive fishing and climate change.

What are the characteristics that make fishing-dependent human communities sustainable and resilient to changes in marine ecosystems? How do the scales of environmental variability, both temporal and spatial, affect the ability of these human communities to identify and respond to this variability? How do the scales of organisation of these communities promote or constrain their ability to respond to environmental variability? These are central questions of

*Corresponding author. Tel.: +1 250 756 7137; fax: +1 250 756 7053.
E-mail addresses: perryi@pac.dfo-mpo.gc.ca (R.I. Perry), r.sumaila@fisheries.ubc.ca (U.R. Sumaila).

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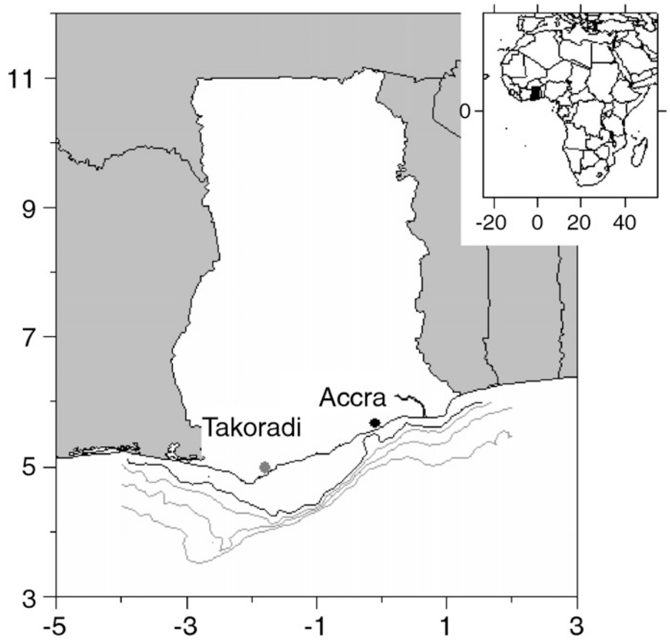

Fig. 1. Map of Ghana, West Africa. Thick dark line indicates the 200 m isobath, lighter lines indicate the 1000, 2000, and 3000 m isobaths off Ghana.

the human impacts of global change, and answering them involves studying the interactions between natural marine ecosystems and human communities, i.e., changes in marine ecosystems affect fishing-dependent human communities, but how these communities respond to these changes also have impacts on the marine ecosystems [1]. The practical method to examine these issues is to use case studies with examples from different natural and socio-economic systems (e.g. [2,3]). In this paper, we provide an overview of variability in the Guinea Current marine ecosystem and the strategies developed by fishing-dependent coastal communities in Ghana, West Africa, to cope with environmental variability.

Ghana (Fig. 1), is a tropical country which has a coastline of 528 km and a continental shelf area of 23,700 km^2. A significant proportion (42%) of the population lives within 100 km and 65% live within 200 km of the coast [4]. Fish is an important source of animal protein, with consumption approximately 22 kg yr^{-1} [5]. Many fish stocks in the Guinea Current region are declining, however. Two key explanations that have been proposed for these declines are environmental variability and fishing [6].

2. Environmental variability

The marine waters of Ghana are located within the Guinea Current Large Marine Ecosystem, and form part of the Central West African Upwelling system. Important environmental variability occurs on seasonal, inter-annual, and decadal scales. Seasonal variability is dominated by upwelling, which has two peaks: December to February (the ''minor'' season) and July to September (the ''major'' season) [7]. Inter-annual variability is related to the basin scale variability of the tropical Atlantic and to large scale atmospheric changes induced by El Niño-Southern Oscillation (ENSO) events in the tropical Pacific Ocean. These events affect upwelling along the Northwestern African coast between 10° and 26°N [8] and in the Guinea Current system off Ghana [9,10]. Sea surface temperature anomalies off Ghana (bounded by 4°–6°N, 3°W–1°E) for the period January to June 1961–2002 (data derived from the Reynolds Sea Surface Temperature (SST) database [11]) are significantly and positively (although weakly) correlated with ENSO activity in the Pacific Ocean (linear regression, $r^2 = 0.10$, $p = 0.04$); in this analysis, ENSO activity is defined by the multivariate ENSO index, MEI [11], for the November–December period of the preceding year. It is not surprising that ENSO modulation of sea surface temperatures off Ghana is weaker than that observed off NW Africa [8] because the Guinea Current ecosystem is not a typical wind-driven upwelling system such as occurs off California, Peru and Namibia. Guinea Current upwelling appears to be controlled by a combination of local and remote processes, the latter having their origins in the western part of the Atlantic basin and being transmitted to the eastern side through the equatorial wave guide.

At inter-annual and decadal scales, environmental conditions in the Guinea Current region, such as sea surface temperatures off Ghana and rainfall in the Sahel region of West Africa, also demonstrate marked variability (Fig. 2a,b). Binet [12] suggested that warm events in the equatorial Atlantic occur every few years, possibly as a consequence of ENSO events in the Pacific. These SST data suggest inter-annual cycles of 3–4 years (confirmed by spectral analyses; data not shown), which is similar to inter-annual variability of the MEI (ENSO events) (Fig. 2c). In addition, there is a decadal scale pattern of cooler sea temperatures from the mid-1960s to the late 1970s, followed by a strong warming trend to 1990 and then more gradual warming (Fig. 2a). This pattern is in general agreement with the climatic periods identified in sea temperature and salinity properties in this area by Koranteng and McGlade [13]. Rainfall in the Sahel region of West Africa (which includes countries to the north of Ghana) also shows a decadal scale pattern with a long period of drought starting around 1970 which reached its deepest extent in the mid-1980s (Fig. 2b; [14]).

Fishery resources in the Guinea Current region include over 300 species of finfish, 17 species of cephalopods, 25 species of crustaceans, and three species of turtles [5]. The most abundant (commercially) have been the small pelagic species such as Clupeidae, Carangidae, and Scombridae, which support significant artisanal and industrial fisheries. Large pelagic species such as the tunas (in particular skipjack, yellowfin, and big-eye) also occur year-round throughout the whole of the Gulf of Guinea; along the coast they concentrate during the major upwelling season and are fished there by seiners [15]. Six different

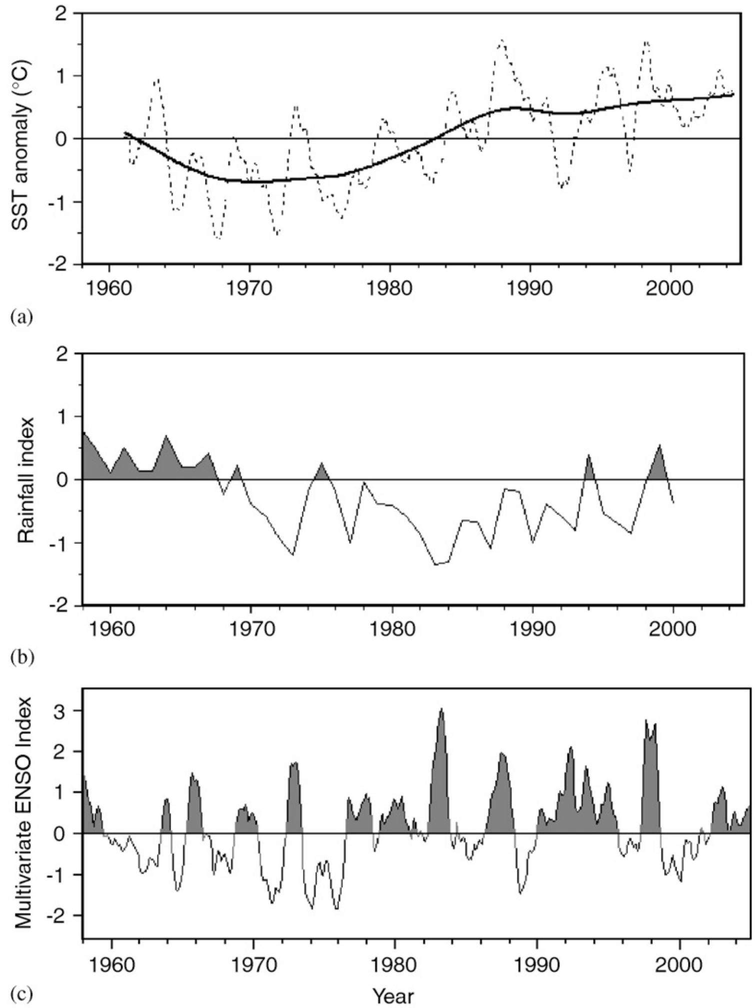

Fig. 2. (a) Annual sea surface temperature (SST) anomalies (dashed line) off Ghana, within the box bounded by 4–6°N, 3°W-1°E [11]. Seasonal variability was been removed prior to calculating the annual averages. Solid line is a smoothing spline applied to these data, with 7 degrees of freedom; (b) Annual index of rainfall in the Sahel region north of Ghana. Redrawn after Ref. [14]; (c) Monthly Multivariate ENSO Index (MEI), smoothed with a 3-month moving average [11].

communities of demersal species have been identified, with distributions based on bottom type and environmental conditions [6]. Commercially important invertebrates include shrimps, lobsters, and cephalopods which tend to be fished only to 75 m because of untrawlable substrates at deeper depths.

3. Human impacts: fishing

Ghana used to be a major fishing nation in West Africa, but the status of the fishing sector has declined over the past four decades [16]. Landings by Ghana have been on average 21% of total fish landings from the Guinea Current system. These data [17] are landings reported annually to the Food and Agricultural Organisation (FAO) of the United Nations, and allocated to the country's EEZ using the method of Watson et al. [18]. Ghanaian landings are dominated (93%) by small and medium sized pelagic fishes and demersal fishes. As with the physical oceanographic conditions, annual recorded landings vary on inter-annual to decadal scales. Landings of pelagic fishes, in particular the anchovy *Engraulis encrassiolus* and the Sardinella (especially *Sardinella aurita*), increased spectacularly in 1972 and collapsed shortly thereafter. They increased again from the late 1970s until the mid-1990s (Fig. 3). The temporal pattern of these landings in Ghana is representative of small and medium pelagic fish landings throughout the entire Guinea Current system, a spatial scale of over 3000 km. Binet [12] suggested that the increased landings during the 1980s may have resulted from stronger and more frequent ENSO events which widened coastal eddies in the Guinea Current thereby increasing survival of larval Sardinella. ENSO-linked warm events during this same period have also been observed to influence Sardinella distributions and catches from Congo to Angola [19]. Landings of demersal finfish off Ghana also increased from 1960 to 1980 but have been variable in recent years (Fig. 3).

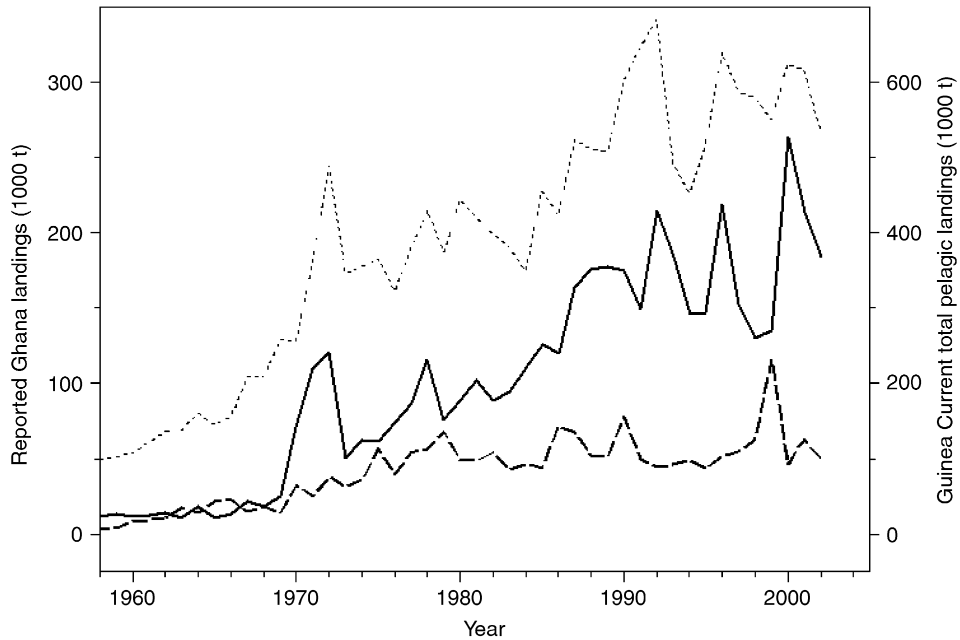

Fig. 3. Reported landings for Ghana of small and medium pelagic (heavy sold line, left axis) and demersal (dashed line, left axis) species. Dotted line (right axis—note different scale than left axis) are total landings of small and medium pelagic fishes throughout the Guinea Current system.

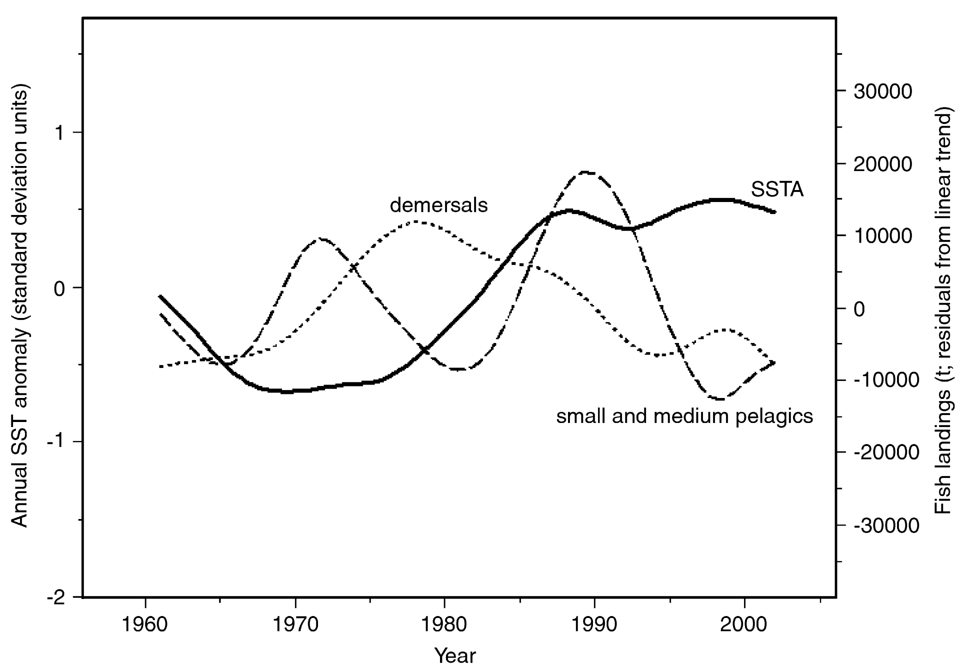

Fig. 4. Annual anomalies of sea surface temperature (SSTA) with seasonal cycle removed (heavy solid line, left axis), and residuals (linear trend of each time series removed) of small and medium pelagic (dashed line, right axis) and demersal (dotted line, right axis) fish landings in Ghana. All series have been smoothed using a spline with 7 degrees of freedom.

There are interesting dynamics (Fig. 4) between annual anomalies of SST and the annual landings of small and medium sized pelagic fishes (with their strong linear trend removed). Landings of small pelagic fishes appear to be unusually large in years with lower sea surface temperatures (i.e. with greater upwelling), although the relationship is not statistically significant (contingency table analysis, Fisher's exact test, $p = 0.06$). This analysis compared differences of SST anomalies against year-to-year differences in the detrended pelagic fish landings, and suggest that when SST anomalies decreased the pelagic fish landings tended to increase. Bakun [9] found that periods

of intense local upwelling were associated with increased local *S. aurita* availability, and with low rainfall along the adjacent coast. There is also a relationship between landings of small and medium sized pelagic fishes and the landings of demersal fishes, such that demersal landings were relatively high when pelagic landings were low (Fig. 4; Fisher's exact test, $p = 0.05$). This relationship is most likely a result of target switching by fishermen when the preferred pelagic species are less abundant.

Demersal fish productivity off Ghana has been relatively high (1.239 t km^{-2}) compared with other upwelling systems (excluding Peru, Chile, Senegal) and positively related to upwelling [7]. Fisheries-independent surveys suggest that demersal fish declines on the order of 50% have occurred from the late 1970s to the 1990s [20–22]. Fully-exploited or over-exploited groups include shrimp and octopus off Senegal and several demersal fish taxa such as Sciaenids, Sparids and Haemulidae (grunts) in the waters of Côte d'Ivoire, Ghana, Togo and Benin [23]. In addition, there have been significant shifts in the composition of demersal species over this period. For example, triggerfish (*Balistes* spp.) were rare in the 1970s, dominated the demersal fish fauna in the Gulf of Guinea ecosystem during the 1980s, but were again rare during the 1990s [24]. At the same time as triggerfish declined, the smooth puffer fish (globefish; *Lagocephalus laevigatus*) briefly increased in abundance but then decreased again despite it not being the subject of a directed fishery [24].

Per capita supplies (national production plus net imports) of demersal fish were greater than that of pelagic fish in the early 1960s, but declined slowly until 1991 (Fig. 5). It has remained relatively stable since 1991 at 2.2 kg yr^{-1}. In contrast, per capita supply of pelagic fish increased dramatically in the early 1970s, declined, and then slowly increased until 1997 after which it has remained at an average of 20.8 kg yr^{-1} (Fig. 5). Since the domestic supply of pelagic fish during the late 1980s and early 1990s was variable but with no discernable trend (mean $\pm$ 1 standard deviation $= 276{,}000 \pm 37{,}000$ t), the increased per capita supply of pelagic fish since 1996 was provided by imports (Fig. 6).

The dominant fishery sector in Ghana is the artisanal fishery conducted mostly from canoes, followed by the industrial and semi-industrial sectors [16]. The number of canoes increased from about 7000 to 10,000 during the period of strong increase in fishery landings from 1980 to 2000 [16]. The sea-going range of canoes also increased due to larger sized boats and increased motorisation [25]. However, an increase in the number of fishers per boat (from 11.1 to 12.4 between 1992 and 2001) and an overall reduction in the catch per boat (from 35 t in 1992 to 23 t in 2001), as well as increasing fuel costs, reduced the role of this sector as a source of significant employment [16]. These difficulties resulted in a rise in unemployment (100,000 jobs were lost in the fishing industry from 1992 to 1996; [26]), in part due to inland drought driving migration into coastal areas (which may be due to recent stronger and more frequent ENSO events, e.g. [9]), and easy mobility in and out of fishing. Such easy mobility can impede the serious regulation of the fishery and the diversification of skills and livelihoods, resulting in over-exploitation and reduced catches [27]. Gender issues are also involved. Fishing crews

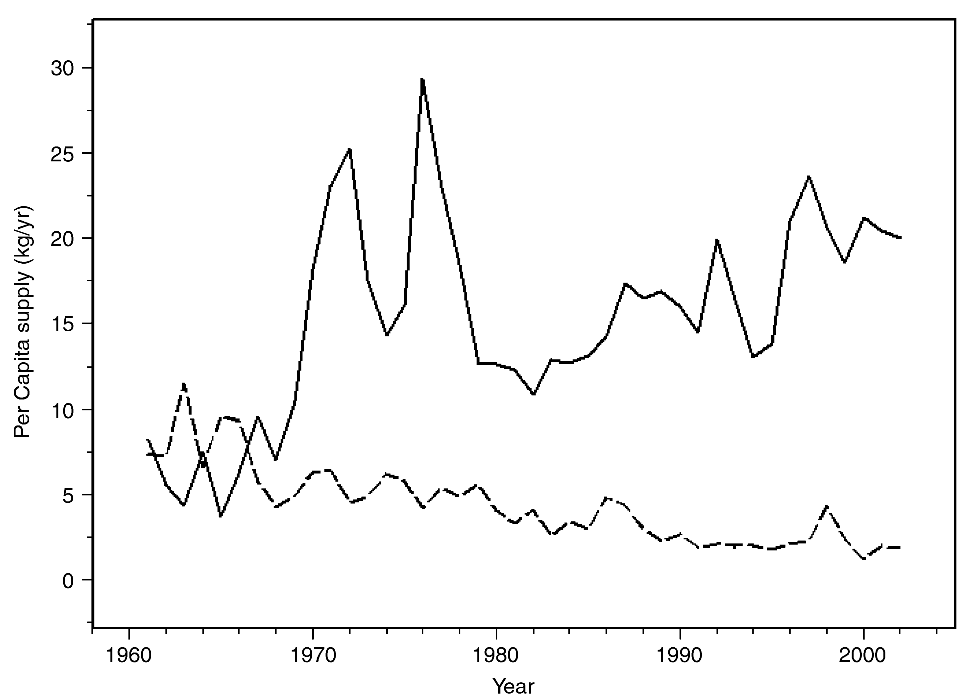

Fig. 5. Ghanaian per capita supply (domestic production plus imports) of small pelagic (solid line) and demersal (dashed line) fish.

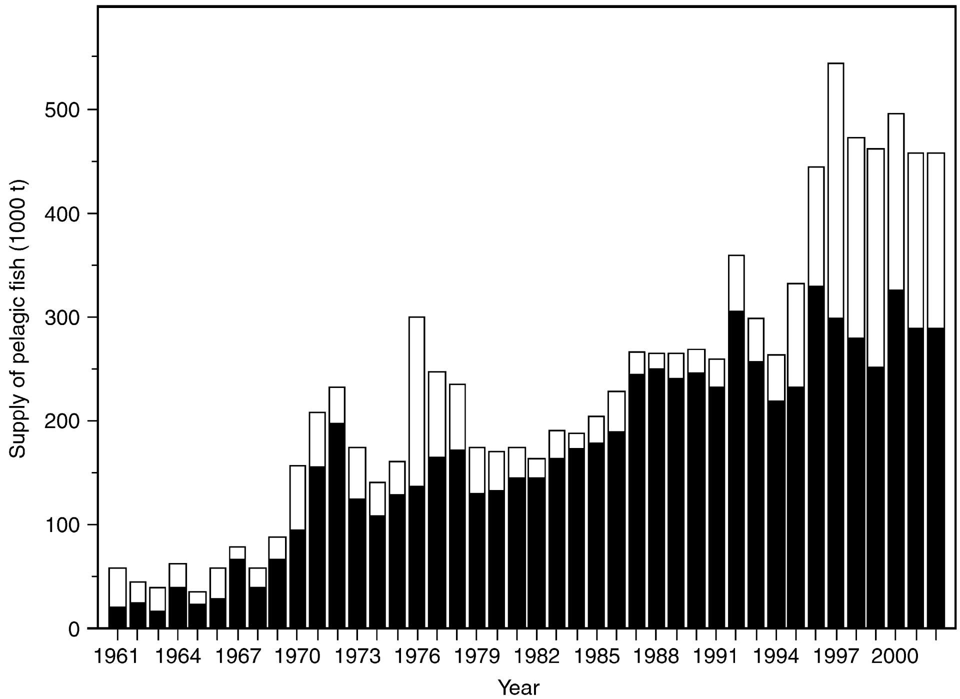

Fig. 6. Domestic production (landings) of pelagic fish (solid bars) and imports of pelagic fish (open bars) in Ghana.

are mostly males who, because they are at sea, have limited time for other economic activities, whereas fish processors and traders are mostly females who, because they work ashore, can participate in a variety of activities [25,28].

Variability in both environmental conditions and fishery landings off Ghana occurs at inter-annual to decadal scales. Using the fishery data, four key periods can be identified:

(1) pre-1970, when reported landings were low and similar between pelagic and demersal species;
(2) early 1970s, during which very large landings of small pelagic fishes occurred, mostly Sardinella spp. but also including the anchovy *E. encrassiolus*, and demersal fish landings were increasing;
(3) 1973–1990, during which landings of both small and medium pelagic species and demersal species increased; and
(4) 1990 to present, during which landings of pelagic and demersal fish species were variable with no discernable trend. In addition, the per capita supply of fish (predominately small and medium sized pelagic species) was kept high in the late 1990s by imports.

Bakun [29] comments on these productive periods, suggesting that the Sardinella boom and subsequent bust in the early 1970s may have resulted from increased availability of small pelagic fish to the fishery, which was not sustainable. In contrast, increased landings from mid-1970 to the late 1980s appear to have been sustainable, at least over several generations of pelagic species. Bakun [29] suggested that ocean productivity may have changed during this period. It is clear that the conditions generating ENSO events in the Pacific Ocean moved into a more active phase in the late 1970s (mean MEI is significantly different before and after 1977; t-test, $p<0.01$, df $=668$), which included two of the largest recorded ENSO events (in 1983 and 1997; Fig. 2c). These periods also correspond to changes in sea surface temperature, which was cool during the 1960s, warmed rapidly through the late 1970s and 1980s, and then warmed slowly during the 1990s (Fig. 2a). These patterns in environmental conditions and fishery landings are suggestive of reduced productivity and perhaps declining stock sizes during the 1990s, in particular of pelagic species, although Koranteng and Pauly [24] report similar declines of demersal fish over this same period. The decreasing supply of fish has led to reduced earnings to the state from licenses and taxes, reduced spin-off economic activities (such as vessel suppliers, fuel sellers) and reduced investment in the fisheries sector leading to a declining contribution of fisheries to the GDP of Ghana [16,26].

4. Livelihood adaptation strategies

Artisanal fishing families have developed a variety of fishing and non-fishing strategies to deal with the influence of seasonal to inter-annual environmental variability on the availability and productivity of small and medium-sized pelagic fishes off Ghana. Fishing families also experience, and must deal with, variability in their social, economic and political environments [20,25]. These strategies involve selecting activities from among the various livelihood

resources or ‘‘capitals’’ [25,30] such as natural resources, networks and partnerships (social resources), skills, knowledge and technical abilities (human resources), infrastructure, equipment and tools (physical resources), and financial resources. Each of these activities have associated with them explicit or implicit temporal and spatial scales, which may or may not match the scales of environmental or social variability.

4.1. Natural resources

When key fish species, such as small and medium sized pelagics, go into decline, the immediate strategies of fishermen are to fish harder, i.e. to fish farther from shore and to spend longer times at sea (thereby increasing risks to human safety) and/or to switch gears to target other species [25]. This latter action can be seen in Fig. 4 in which the decline of pelagic fish landings is followed by increases in landings of demersal species. The result, however, can be increased conflict among fishermen using different gears on an already crowded continental shelf [24], and can lead to destructive fishing practices such as the use of dynamite [25]. The ability to switch gears to catch other species also depends on the skills of the fishermen (human resources) and economic conditions (financial resources). When fish stocks declined during the late 1990s, other species apparently were left un-exploited [31]. This may have been due to an inability to invest in new gear for these fisheries because of national economic hardships which increased costs and decreased purchasing power during Ghana's structural adjustments at this time [31].

An important secondary strategy for fishermen when local catches are reduced is to undertake seasonal fishing migrations. Ghana has a tradition of its artisanal fishermen fishing in the waters of other West African countries, in particular Côte d'Ivoire, Togo and Benin [26]. From the mid-1970s to the mid-1980s, catches and landings by Ghanaian fishermen in adjacent countries ranged between 20 and 30% of the total annual West African landings (Fig. 7; excluding Ghanaian catches landed in Ghana). This proportion increased to about 50% by the late 1990s but has fallen to below 30% since 2000 as these countries began to exclude Ghanaian fishermen from their domestic waters. The livelihood strategy of 'migrating to follow the fish' over regional spatial scales is therefore being constrained by political actions from outside of Ghana.

Declines in the availability of fish can result in increased exploitation of terrestrial ecosystems. Smoking is an important method to preserve fish because of a lack of ice; with a decreased supply of fish, smoking is used to extend its preservation. Increased smoking, however, increases the removal of trees in the vicinity of villages [27]. The consumption of bushmeat (wild animals) in Ghana is common, and can be an important source of protein both in rural and urban areas [32]. Its availability and price varies with species and method of preservation, and in large coastal centers such as Sekondi–Takoradi it can be more expensive than domestic meat or fish. The annual national estimate for bushmeat consumption in Ghana is 14.5 kg/person [32], compared with about 22 kg for fish. However, Brashares et al. [21] have reported an important link between seafood supply and bushmeat

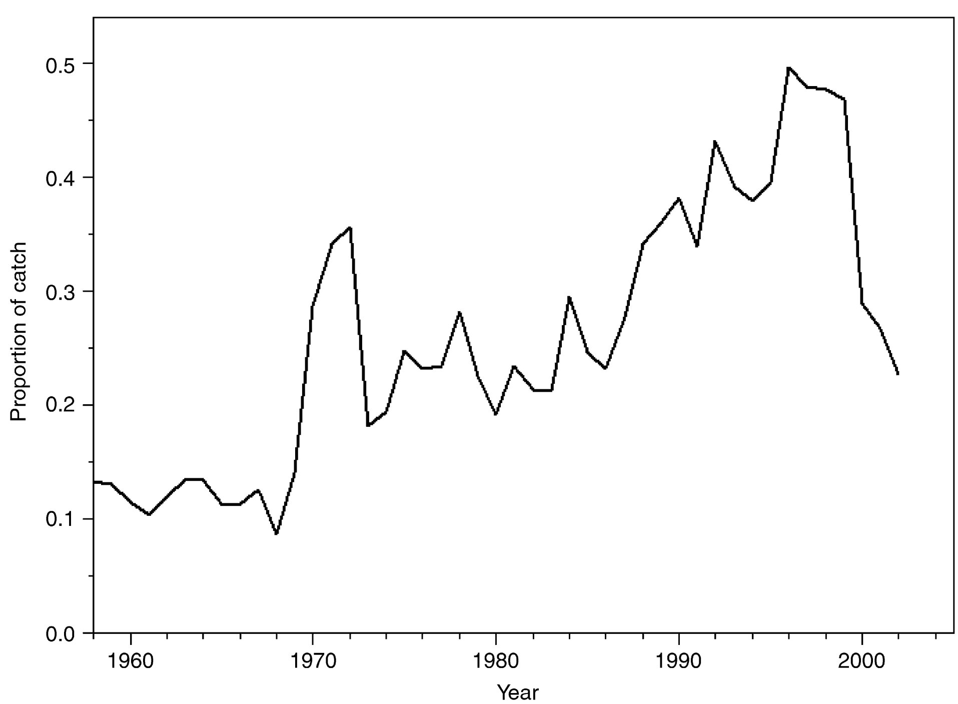

Fig. 7. Proportion of total landings that Ghanaian fishermen contributed in other West African countries (Sierra Leone, Liberia, Côte d'Ivoire, Togo, Benin), excluding Ghanaian catches and landings in Ghana itself. Data from Sea Around Us Project [17].

hunting. Years of poor fish supply have coincided with increased hunting of wild animals (bushmeat) in nature reserves in Ghana and led to declines in biomass of 41 wildlife species over the period 1970–1999 [21]. Correlations between fish supply and wildlife declines are strongest in nature reserves closer to the coast. Brashares et al. [21] suggest that fish and bushmeat supplies are related through market forces, such that when the supply of fish is reduced, its price increases and it is replaced as a protein source by the hunting and consumption of bushmeat. This process can be thought of as a livelihood strategy involving prey-switching by the consumer, similar to switching by fishermen between pelagic and demersal fish species but in a marine–terrestrial context.

4.2. Human resources

Gender differences play an important role in livelihood adaptation strategies [33]. Multiple income strategies which spread risk, such as males doing the fishing and females the processing and trading (which can involve receiving fish from more than one fisherman), are important for building resilience to environmental variability [25]. Women's control over fish buying and processing (e.g. smoking) provides them with income that can be used for investment [28], and also a product that can be sold beyond the fishing season. Since women mostly remain at home, some invest in small produce farms, in particular during seasons of poor or no fishing [27].

4.3. Social, physical, and financial resources

Artisanal fishing families have traditionally built social relationships and groups (communities) to improve their economic security, so that friends and relatives provide a safety net for (at least) short periods of tough times. They may also change the extent of their investments in fishing, by reducing the number of boats that they operate or downsize from industrial vessels to artisanal canoes. They may further reduce their exposure to fishing by investing their assets in land or other businesses [25]. Nationally, when the domestic production of fish declines the supply of fish per capita can be kept high by expending national financial capital to import fish (e.g. Fig. 6).

Migration of fisherfolk within and outside of Ghana has been a key response to natural resource variability [31], and one that operates at several spatial and temporal scales and involves several livelihood strategies (at least social, human, and financial). Most common "non-permanent" migration is by fishermen to distant fishing grounds, often in the national waters of other countries. Fifty percent of migrants go on short-term trips of 1–3 months, following the seasonal availability of the fishery resources (mostly the small-medium sized pelagic species). Marquette et al. [31] suggested that historically there is little evidence that migration of fishers along the coast was due to local population pressure or to local over-exploitation of fish resources. Instead, the forces that encouraged migration tended to be economic opportunities and the seasonal availability of fish. Migration has therefore become an integral part of the fish production system, making this system rather resilient to population growth, fish stock variability, and national economic decline [31]. Migration provides a means to become a professional fisherman or fish trader, and provides access to natural, economic, and social resources beyond the local community which can be re-invested at home [31]. However, this strategy may now be at risk as adjacent countries begin to exclude Ghanaian fishermen. The increase in landings by Ghanaian fishermen in other West African countries during the late 1990s (Fig. 7) was in large part driven by landings in Sierra Leone and Liberia, much farther west than Ghanaian fishermen have previously fished extensively. At longer time scales, "semi-permanent" to "permanent" migrations can occur from rural to urban environments, resulting in increased social problems in the cities [16].

5. Discussion

The changes that have occurred in the marine ecosystem off Ghana undoubtedly result from the combined impacts of a changing environment and fishing. Environmental variability sets the background on which fishing is imposed as an added forcing. The variability that is observed off Ghana in environmental conditions and fishing is representative throughout inland terrestrial environments (the Sahel region) and much of the Guinea Current system, stretching from Guinea to the Congo. It results from atmospheric forcing at large inter-ocean scales. It is important to understand how human livelihood strategies which are locally, or at times regionally, focused interact with environmental variability at such large spatial scales in order to encourage fishing families to select among the more sustainable strategies. In addition, livelihood strategies may be well-adapted to seasonal and perhaps inter-annual temporal variability in environmental conditions, but may be poorly adapted to variability at longer (e.g. decadal) scales.

Fishing-dependent human communities in Ghana are challenged by economic and natural resource availability issues on a variety of temporal and spatial scales. The largest sector of the fishery is the artisanal fishermen. They have developed a variety of fishing and non-fishing livelihood strategies to respond to high seasonal to inter-annual variability of small and medium sized pelagic fishes. Particular strategies include exploiting natural resources more intensively, both directly and indirectly. Direct exploitation involves fishing harder, such as exploring other areas perhaps deeper and further offshore which had been lightly fished, migrating to distant fishing grounds, and switching to alternative species. These alternative species often include demersal species, however, this option may become closed as demersal populations also go into decline. Indirect exploitation involves increased

exploitation of terrestrial systems as market forces intervene to increase the prices of various sources of animal protein. Non-fishing strategies include dependence on social networks for support, at least in the short-term, transferring investments outside of fishing and its related activities, and/or moving to larger urban centers to seek work.

Livelihood strategies which might appear to be sustainable at local time and space scales may not be sustainable at larger scales. All these livelihood strategies have negative impacts to the natural environment associated with them. Fishing harder exploits fish in what might previously have been refuge areas; targeting other species or using destructive fishing techniques spreads the negative impacts of fishing to other components of the ecosystem; and migrating to distant fishing grounds spreads the impacts of fishing spatially. If these other fishing grounds are within the same large marine ecosystem (the Guinea Current system) they are likely to be already experiencing similar environmental variability as off Ghana. Increased hunting of wild animals (bushmeat) in terrestrial systems may impose additional stress on these ecosystems which may also be experiencing environmental changes, e.g. reduced rainfall. Migration into cities also imposes further stress onto already over-stretched urban social systems.

Fishing, and fishery management strategies, need to take account of and be adjusted for favourable or unfavourable environmental conditions. Selection of appropriate scales of analysis is an important consideration [1]. The processes driving environmental variability in the Guinea Current system operate at very large, even global, spatial scales. Both the inter-annual variability in SST and its decadal scale pattern off Ghana appear to be influenced by ENSO events in the tropical Pacific Ocean and by variability in the tropical Atlantic. These processes are also likely to affect the entire tropical west coast of Africa [19] and terrestrial ecosystems in West Africa through changes in rainfall. In contrast, the livelihood strategies employed by coastal communities to respond to environmental variability have local, regional, and national spatial dimensions. Regional spatial scales are involved when fishermen migrate to distant fishing grounds, but these options may be closed due to political issues in the host country or because these grounds are also negatively affected by the large-scale natural variability. At the national scale, shortfalls in the supply of fish can be made up by increasing imports of fishery products; the general national economic situation will also enhance or constrain several of the livelihood strategies. At the local scale, the natural, social, human, and financial opportunities of each fishing village provide different suites of livelihood strategies for fishing families and their communities.

In conclusion, the upwelling marine ecosystem off the coast of Ghana undergoes natural environmental variability on a variety of time scales that is linked to global processes. The coastal human communities which exploit and depend on this ecosystem have developed a number of strategies to maintain their resilience against this variability. These form a linked social–ecological system which is bi-directional: changes in the marine ecosystem can affect human communities, and changes in human communities can affect the marine ecosystem [34] or beyond to terrestrial ecosystems. Traditional livelihood strategies, in particular those involving natural resources, are best adapted to short-term (inter-annual) variability. They can break down if the characteristics of the environmental variability change, such as when low frequency decadal scale variability dominates (“regime shifts”) and/or when the resilience of natural systems is exceeded by over-exploitation. When studying linked systems of marine ecosystem variability and human responses, it is necessary to consider both small and large temporal and spatial scales.

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